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VARIATION IN THE HELIANTHUS EXILIS-BOLANDERI COMPLEX: A REEXAMINATION

A. M. Olivieri* and S.K. Jain

Department of Agronomy and Range Science
University of California, Davis 95616

In his classic monograph on the evolution of *Helianthus annuus* L. and *H. bolanderi* Gray, Heiser (1949) analyzed variation in natural populations as well as artificial hybrids that led him to the following conclu-

* Present address: Istituto di Agronomia, Universita di Padova, Padova, Italy.

sions: "Of the entities comprising *H. bolanderi,* the one Gray designated *H. exilis* appears to be confined almost exclusively to areas of serpentine outcrops in many of the foothills regions of California, whereas true *H. Bolanderi* occurs in the valleys as a weed. The two races of *H. Bolanderi* conform to the definition of the "ecotype" of the experimental taxonomist." Heiser (1949) discussed the role of introgressive hybridization between *H. annuus,* an introduction into California by the American Indian in recent times, and *H. bolanderi* (native foothills race). Accordingly, he provided a taxonomic key for the two races of *H. bolanderi, annuus* x *bolanderi* hybrid swarms, and for the western races of *H. annuus*. A hybrid swarm between *H. annuus* and *H. bolanderi* was extensively studied by Stebbins and Daly (1961) in which a hybrid index based on six morphological traits was used to analyze population changes over an eight–year period. Although Heiser (1949) raised issues about the definition of species boundaries and the tentative nature of his conclusions regarding the role of introgression, and later (Heiser, 1973) concluded that "no additional evidence has appeared to support or to reject the hypothesis of the origin of the weedy race of *H. bolanderi* through introgression," the sunflower story is frequently cited as an outstanding example of introgression (e.g. Grant, 1971; Briggs and Walters, 1969).

Here we shall briefly reexamine evidence from population studies of two races of *H. bolanderi* (the *exilis–bolanderi* complex) and weedy *H. annuus* in relation to certain systematic, genetic, and statistical aspects of introgression. Morphological variation for a wide range of characters and in three new collections of *H. exilis* provided the basis of a multivariate analysis of these taxa. Preliminary data from the electrophoretic assays of allozyme variation are presented as a test of specific gene transfers through introgression. Two other lines of study, namely, the cytogenetics of hybrid swarms and the ecological tests of the adaptive role of gene exchange, will be discussed in another paper. It should be noted that introgression resembles the common backcross method of plant breeding, and therefore detailed analyses of introgresive hybridization are of wide interest in both evolution and crop genetics.

Materials and Methods

Fourteen populations were sampled during the summers of 1973, 1974 and 1975 by harvesting 50–100 individuals along two or three linear transects per population (Table 1). Twenty to 75 plants were scored for plant height*, branching index (1 = none to 5 = extensive branching), stem diameter, stem pubescence*, stem color (1 = green to 4 = red), number of opposite leaf pairs, number of unpaired leaves*, leaf length*, and width*, leaf shape index* (1 = linear, 5 = cordate), leaf margin

* Characters marked by an asterisk were also scored by Heiser (1949).

TABLE 1. SPECIES AND PROVENENCE OF THE POPULATIONS STUDIED.

	Species	Locality	Code	No. of plants studied
annuus	1. H. annuus	Yolo Bypass; 0.5 mi. S of 1st bridge of I-80 from Davis to Sacramento.	DVS 1	24
annuus	2. H. annuus and H. annuus x H. Bolanderi	40 meters N from site DVS 3, across the railways.	DVS 2	33
exilis	3. H. Bolanderi	About 3 mi. NW of Knoxville (located N of Lake Berryessa), off Berryessa-Knoxville Road and along Cedar Creek Road.	KNX 1	20
exilis	4. H. Bolanderi	1.5 mi. W of KNX 1, near Hunting Creek.	KNX 2	42
exilis	5. H. Bolanderi	Patch located near the Campground, about 50 meters from KNX 2.	KNX 2a	20
valley *bolanderi*	6. H. Bolanderi	4 mi. S of Williams Colusa Co., along Rd. 15.	WLS	32
valley *bolanderi*	7. H. Bolanderi	4 mi. W of West Butte, Sutter Co., along Pass Road.	WBT	46
valley *bolanderi*	8. H. Bolanderi	2.5 mi. NW of Sutter, Sutter Co., along Pass Road.	STR	39
	9. H. Bolanderi and H. Bolanderi x H. annuus	5.4 mi. E of Davis, Yolo Co., in ditch area between railways and Frontage Road along 180.	DVS 3	75
foothills *bolanderi*	10. H. Bolanderi	About 7 mi. NW of Knoxville, off Morgan Valley Road.	KNX 5	36
foothills *bolanderi*	11. H. Bolanderi	About 5 mi. NW of Knoxville, along Morgan Valley Road.	KNX 7	33
foothills *bolanderi*	12. H. Bolanderi	3 mi. NE of Middletown, Lake Co., along S29.	MTW 1	26
foothills *bolanderi*	13. H. Bolanderi	4 mi. NE of Middletown, Lake Co., along S29.	MTW 2	28
foothills *bolanderi*	14. H. Bolanderi	ca. ½ mi. N of KNX 2, along Hunting Creek.	KNX 3	22

dentation (1 = none, 3 = extensive), head diameter*, disk diameter*, number of ray flowers*, ray width, ray flower shape, floret length, floret tube length, basal floret shape index* (1 = not swollen to 3 = largely swollen), floret color (1 = yellow, 2 = light red, 3 = dark red), stigma apex color (1 = yellow, 2 = orange, 3 = red), lateral and central palea

cusp length, palea apex color, involucral bract number, bract length* and width*, bract pubescence*, achene length* and width*. Numerical taxonomic analyses of vegetative and floral characters were carried out with a BMD principal component analysis program.

Samples of populations KNX 1, KNX 2, DVS 1, and DVS 2 were grown during 1975 summer in the greenhouse in 18 cm pots and UC soil mix, and scored for a subset of 15 characters to study population differances under a common environment. To measure the genetic similarities among different groups of populations, electrophoresis for isozyme variation was carried out using standard horizontal starch gel techniques described by Shaw and Prasad (1970), with minor changes to adapt to our materials. Three– to four–week–old seedlings were used for sample extracts. Three enzyme systems (leucine aminopeptidase, phosphoglucomutase, phosphoglucose isomerase) were scored. Data on the allelic composition at two alcohol dehydrogease loci were kindly supplied by Dr. A. Torres of the University of Kansas on a small set of samples. For present purposes, a phenotypic analysis of variation is presented in terms of the presence vs. absence of well–developed and consistent bands within populations, rather than gene frequencies, since genetic analyses using progeny tests are not yet completed for most of the loci. Accordingly, data are summarized in terms of the number of different alleles present in several populations, and estimates of similarity are based on Jaccard's index, $J = \frac{c}{a + b - c}$, where c = number of common alleles between populations A and B; a and b are total numbers of alleles in populations A and B respectively.

Results and Discussion

Means were determined for 15 characters and ten selected populations based on the field samples (Table 2). Heiser (1949) had noted that important taxonomic distinctions were based on the shape of involucral bracts, the nature of the palea or chaff (length, texture and angle of awn of the palea or chaff), and the overall size of the plants. Leaf shape, disk diameter, ray number, and achene length were included in his "taxonomic key features" (Heiser's Table 1). Our data confirm his observations on these characters for describing the two *H. bolanderi* "ecotypes" and weedy *H. annuus* (Table 2). However, it should be noted that our *H. exilis* populations are a distinct group based on the same characters and in fact represent an extreme below the following ranges for the foothills *H. bolanderi:*

TABLE 2. ESTIMATES OF CHARACTER MEANS FOR 10 SELECTED POPULATIONS

Species and location	H. annuus		H. bolanderi						H. exilis	
			valley			foothills				
Character	DVS 1	DVS 2	WBT	STR	DVS 3	MTW 1	MTW 2	KNX 5	KNX 1	KNX 2
Plant height (cm)	87.5	108.8	60.7	55.6	30.3	65.3	50.6	39.1	24.4	24.1
Branching index	2.6	2.5	2.1	2.6	1.3	3.1	2.1	2.6	2.7	2.2
Leaf length (mm)	89.0	88.5	50.0	49.6	26.0	64.0	48.6	52.0	28.0	40.0
Leaf shape index	4.7	4.2	3.4	2.8	3.1	2.5	2.9	3.0	3.8	3.9
Head diameter (mm)	62.9	64.7	49.0	47.0	38.7	41.7	44.8	42.4	29.7	26.1
Disk diameter (mm)	17.6	18.6	15.5	13.8	9.4	13.6	12.3	11.4	7.7	7.1
Ray number	13.3	13.9	12.3	11.4	9.3	10.8	10.7	9.6	6.8	7.7
Floret length (mm)	7.5	6.9	6.3	6.3	5.8	5.7	5.8	6.1	5.3	4.6
Basal floret shape index	3.0	2.7	2.0	1.8	1.9	1.4	1.4	1.3	1.6	1.3
Apical stigma color index	3.9	3.7	2.4	2.0	1.7	1.0	1.0	1.1	1.0	1.2
Bract length (mm)	12.3	11.6	12.3	11.9	9.6	11.4	11.2	12.4	8.8	8.5
Bract pubenscence index	1.4	1.7	2.5	2.7	2.6	2.8	2.9	3.0	3.2	2.6
Seed length (mm)	5.4	5.1	4.1	4.3	3.8	2.9	3.2	3.3	2.8	2.5
Seed width (mm)	2.6	2.4	2.1	2.1	2.0	1.5	1.6	1.8	1.6	1.3

	plant height	disk diameter	bract width	ray number	achene length
serpentine, foothill race (á la Heiser)	30–100 cm	15–20 mm	30–40 mm	10–13	3.0–4.0 mm

All three populations from new locations for what we have designated as *H. exilis* group are homogeneous, different, and fall below the ranges given for the foothills *bolanderi* populations (cf. Jain et al., 1977 for agronomic traits in *H. exilis*). Apparently, these localities were not visited by Heiser; the access road to these populations on the Bureau of Land Management land was completed ten years ago. Several of the localities described on the University of California, Berkeley herbarium specimens for *H. exilis* were revisited in 1974. A majority have very small populations and showed a variation pattern in agreement with that described by Heiser (1949) for the *H. bolanderi* group.

Analyses of intrapopulation variation are of particular interest. A nested analysis of variance showed that (1) the *H. annuus* and *H. bolanderi* populations are significantly different ($P < .05$) for 20 out of 21 characters tested; and (2) populations of each of the two species are also significantly different for 18 characters at $P = .01$ and two characters at $P = .05$ levels. Estimates of the coefficients of variations (CV) for a majority of characters were higher in the valley *H. bolanderi* and weedy *annuus* groups than for the foothills *H. bolanderi* or the *H. exilis* populations.

Figure 1 compares the means and ranges (as well as the estimates of standard deviations) for *H. exilis* vs. the two *H. bolanderi* groups pooled together. The ranges overlap considerably but the *H. exilis* means were consistently different from those of *H. bolanderi*. Diagnostic keys in such cases would clearly require a numerical taxonomic approach as well as a further search for certain qualitative genetic traits.

Principal component analysis for vegetative and floral characters respectively reveals that populations 3, 4 and 5 representing *H. exilis* form a separate group, DVS 1 and DVS 2 representing *H. annuus* as a second distinct group, and the remainder *H. bolanderi* populations form a continuum between them (Figs. 2, 3). Populations 10–14 represent the foothills race of *H. bolanderi* which are separated from the valley race (represented by the populations WLS, WBT, STR). Population 9 (DVS 3) represents a hybrid swarm studied by Stebbins and Daly (1961) which was recently fragmented by cultivation and road construction. It seems to be differentiated from all others in its vegetative characters. Overall, the multivariate analysis confirms the observations of Heiser and ours on the four overlapping groups identified in these collections (Table 1). Moreover, data from greenhouse materials of KNX 1, KNX 2

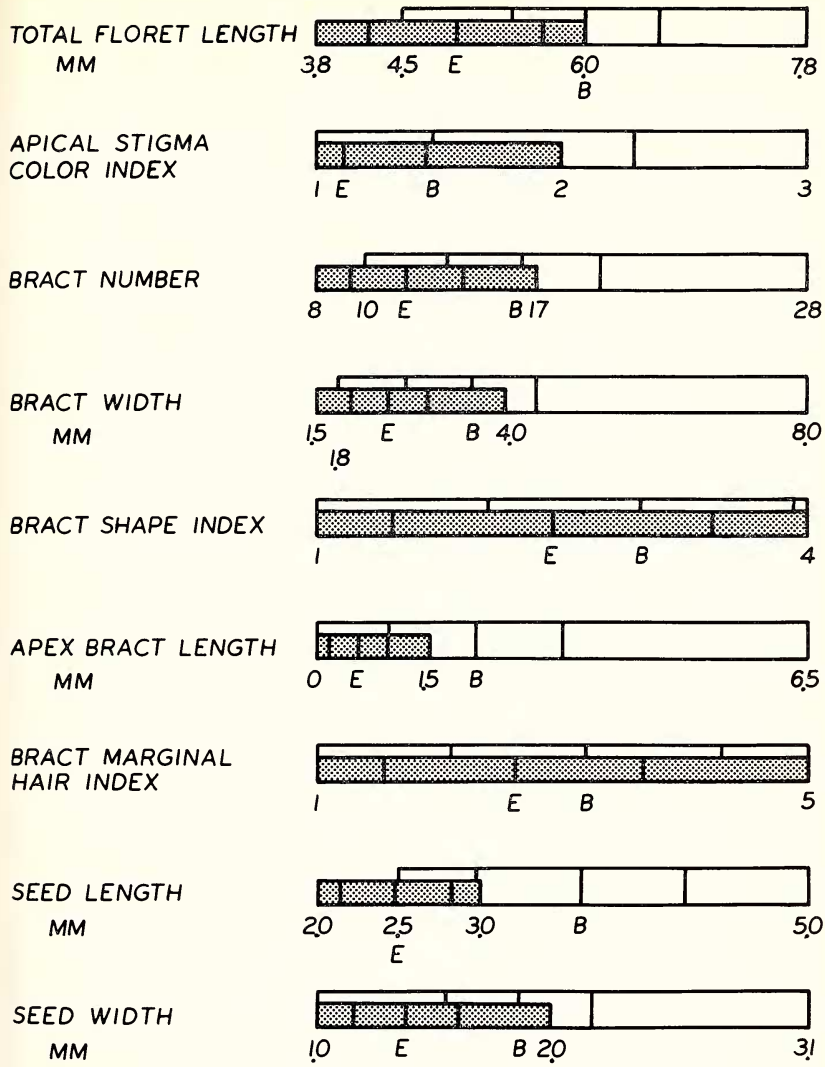

FIG. 1. Range of variation in *H. exilis* (E, stippled area) vs. *H. bolanderi* (B, nonstippled area). Bars near E or B indicate the means and the two bars placed on each side of the means indicate standard deviations. Note the distinctness of *H. exilis* on the basis of range as well as the lower extremes for several characters.

vs. BGS *vs.* DVS 1 and DVS 2 gave significant intergroup differences in a majority of the same characters. Thus, populations as grouped here seem to represent genetically differentiated clusters. Introgression, on the other hand, is neither supported directly nor ruled out by these observations. Valley *H. bolanderi* and weedy *H. annuus* are most likely connected by a

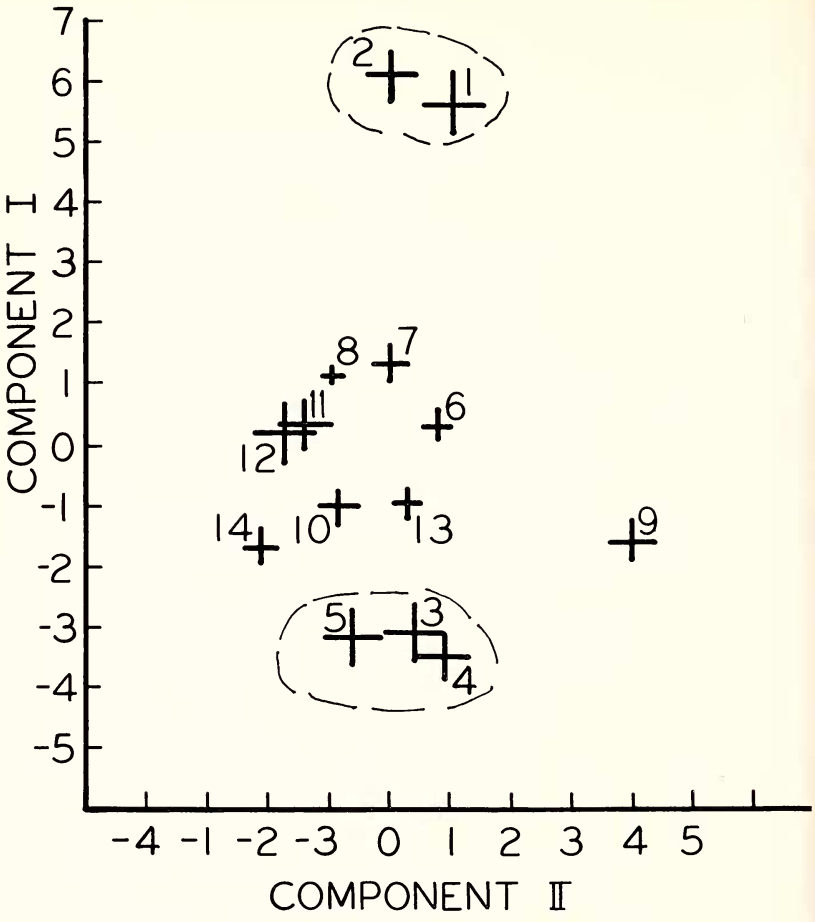

Fig. 2. Principal component analysis of 14 OTUs (Operational Taxonomic Units) using stem, leaf, and seed characters. The codes of locations (1 to 14) are given in Table 1. Dotted boundaries around the four groups of OTUs are drawn simply to match with the four "taxa" as noted in Table 1. No. 9 is an outlier (see text).

series of gene exchange events, and *H. bolanderi* and *H. exilis* in the foothills probably represent another series of populations connected by a two–way introgression underlying the origin of variation in *H. bolanderi*. On the other hand, native *H. exilis* might have been highly variable and could have colonized some disturbed areas on its own. A complete description of parental forms uncontaminated by hybridization is a prerequisite to the "proof" for introgression, and as noted by Heiser (1973) in a recent review, reliance on simply circumstantial evidence is not sufficient.

The so–called hybrid index method is often used to establish introgression (e.g. Keeley, 1976). In this method a set of diagnostic charac-

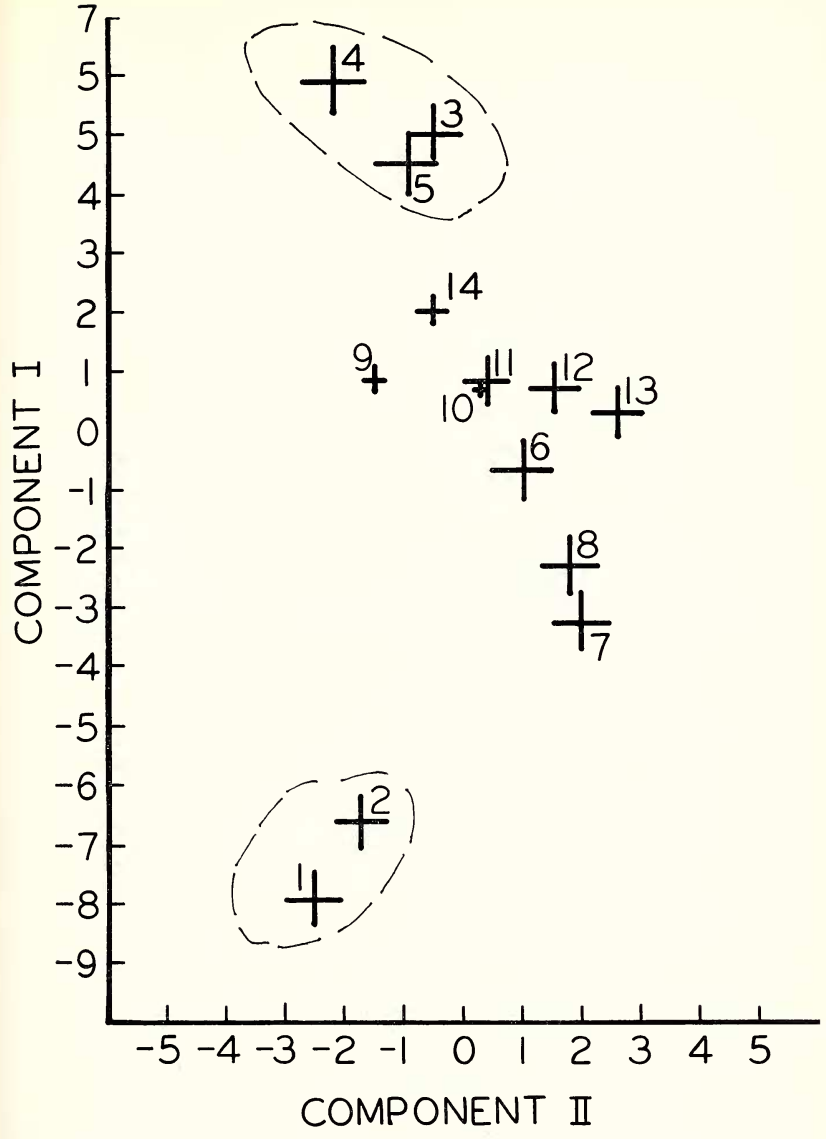

FIG. 3. Same as in Fig. 2 except for the use of floral characters. Note the same four groups, in particular, the separation of *H. annuus* (1,2) and *H. exilis* (3,4,5) from each other.

ters are often selected to pictorialize the variation in putative hybrid swarms. If they vary in a way to show a large amount of overlap with one of the parents but with a few characters from the other parent, introgression is assumed. Many of the examples perhaps show this con-

vincingly, but as noted recently by Namkoong (1966), several statistical and genetic assumptions are rarely stated, much less tested. For example, the number of populations required and the statistical differentiation of hybrid index scores are fairly stringent conditions. Additive genetic variation, independence of different traits, etc. are also assumed. We developed hybrid indices (or what we prefer to call "species identity scores" (SIS) since hybridity need not be presumed) using nine characters chosen to include the six characters (Fig. 4) used by Heiser (1949) and Stebbins and Daly (1961) in their studies and to represent a highly heritable and more or less correlated set of nine traits (Fig. 5) in which case the distributions of DVS 1 and DVS 2 become wider and so also for the WBT population of *H. bolanderi.* The overall gradient across four groups still remains consistent. Use of t–test for significance showed SIS means to be significantly different among various groups, with a larger difference when we used SIS based on the nine correlated traits (Fig. 5). Further weighting by their respective heritability estimates obtained from a greenhouse study (Olivieri, 1976) confirmed that differentiation is at least partly genetic. Use of more characters with known genetic control should improve the interpretation of the SIS scores.

Electrophoretic assays provided a series of isozyme markers (presence vs. absence of bands on gels). Zymograms are drawn to derive the allelic designations for various phenotypes. For alcohol dehydrogenase, surprisingly, *H. exilis* and two cultivated varieties of sunflower had the same alleles whereas *H. bolanderi* showed two unique alleles (A. M. Torres, pers. comm.). For the other three enzyme systems our data are summarized in Table 3. *H. exilis* (KNX 1 and KNX 2) have unique alleles at four out of the eight loci whereas *H. bolanderi* populations have a great deal of variability in both foothills and valley populations but with fewer "unique" alleles. The estimates of Jaccard's index based on the shared alleles between groups taken pairwise are as follows: (a) *H. exilis* vs. foothills *H. bolanderi:* 0.63; (b) *H. exilis* vs. valley *H. bolanderi:* 0.57; (c) valley vs. foothills *H. bolanderi:* 0.69. These estimates are based on very small samples (20 plants per population, two populations per group) and should be considered preliminary. However, so far there is no convincing evidence to reject or accept the hypothesis that the foothills race of *H. bolanderi* is more similar to *H. exilis* due to gene exchange. With further genetic work on allozyme loci and extensive enzyme assays of our collections, this method might yield a crucial test for the postulated gene exchanges between different taxa.

For genetic variation analyses to be useful in a specific test of introgression hypothesis, the key criteria, as outlined by Heiser (1973), include increased hybridity and genetic variation, frequently through the occurrence of a few alleles characteristic of species A in the populations of species B living in the areas of sympatry and habitat changes in recent past. Experimental hybrids and backcrosses could provide some clues to

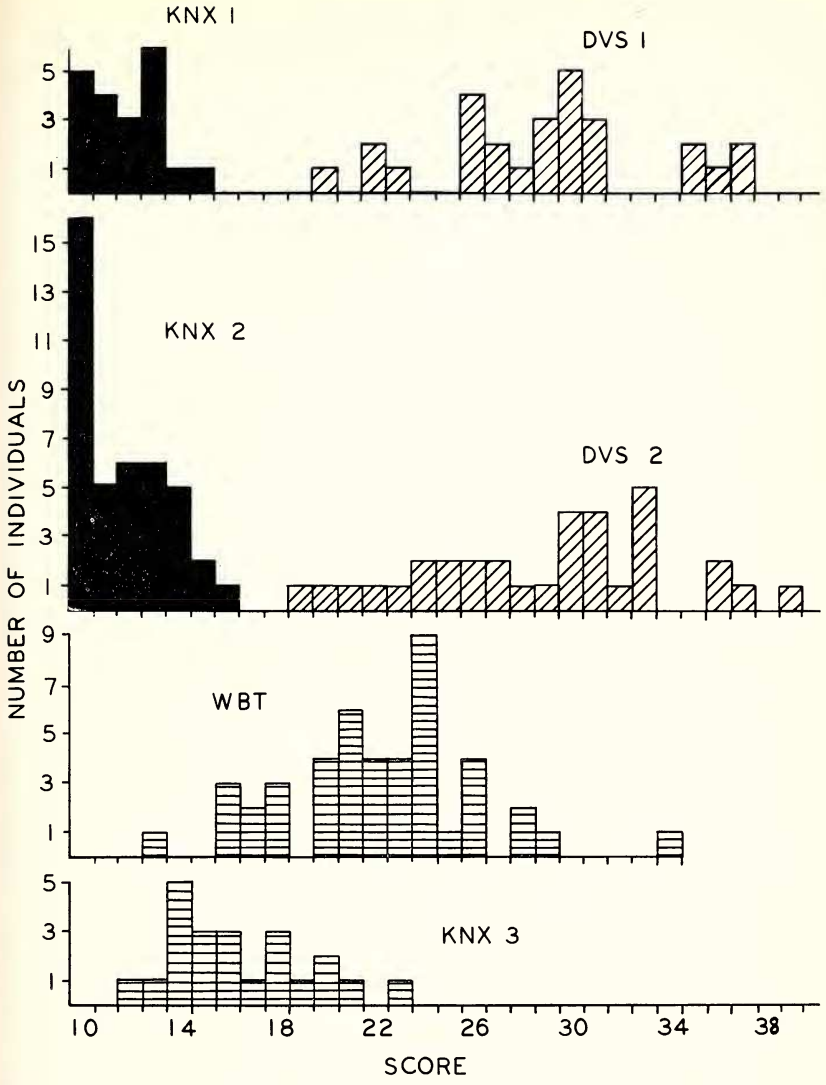

FIG. 4. Histograms showing the frequency distributions of "species identity scores" (= hybrid indices) based on the six characters used by Heiser (1949) in his earlier studies.

the potential for gene exchange as well as to the genetics of species differences. For example, Rick (1969) developed a test for controlled introgression in tomato (*Lycopersicon–Solanum*) crosses using recombination data in the marked regions of three chromosomes. Wall and Wall (1975) developed an experimental test in *Phaseolus* species based on allozyme

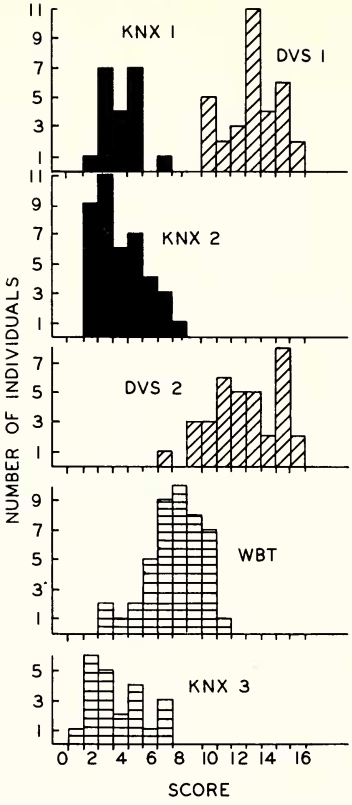

FIG. 5. Same at in Fig. 4 except for the use of nine most highly correlated traits, namely, plant height, leaf shape, stem diameter, diameter of head and disk, ray number, bract number, bract length and bract width. Note that the pattern of distribution is slightly changed toward a wider range and less overlap between the scores for *H. annuus* (DVS1, DVS2) and *H. exilis* (KNX1, KNX2).

TABLE 3. GENETIC VARIATION AT ALLOZYME LOCI.

Enzyme locus	Number of alleles: exilis total	exilis "unique"	foothills bolanderi total	foothills bolanderi "unique"	valley bolanderi total	valley bolanderi "unique"
*Pgm-1	2	1	1	0	1	0
Pgm-2	2	0	2	0	2	0
Pgm-3	3	1	2	0	2	0
*Lap-1	3	1	3	0	3	1
Lap-2	1	0	1	0	2	1
Lap-3	3	1	3	1	4	0
*Pgi-1	1	0	1	0	1	0
Pgi-2	1	0	2	1	2	1

surveys. Several other recent reports (e.g. *Sorghum–Saccharum;* maize–teosinte) have recently appeared in the crop science literature. The results of this study show that evidence for introgression needs to be examined in relation to morphology, Mendelian loci, quantitative genetics of distinguishing characters, and appropriate statistical tests of differences among various taxa. Hopefully, the sunflowers will provide some very exciting materials for population studies on the role of hybridization in plant evolution.

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A NEW COMBINATION IN CYMOPHORA (COMPOSITAE: HELIANTHEAE: GALINSOGINAE)

Judith M. Canne
Department of Botany and Genetics, University of Guelph
Guelph, Ontario, Canada N1G 2W1

Specimens of *Tridax* L. and *Cymophora* B. L. Robins. were examined by the author during studies of the generic and specific relationships of *Galinsoga* Ruiz & Pavon (Canne, in press a, b). A recent, additional study of several specimens of the relatively poorly known *Tridax venezuelensis* Arist. & Cuatr. indicate that this species falls within the concept of *Cymophora* as discussed by Turner and Powell (1977). The transfer of *T. venezuelensis* to *Cymophora* is made here and comments are included concerning interspecific relationships in *Cymophora*.

Tridax venezuelensis shares features of the pappus, achenes, and capitulescence with *T. dubia* Rose and *Cymophora accedens* (S. F. Blake) Turner & Powell while resembling *Galinsoga* in several vegetative and floral features (Aristeguieta, 1964; Powell, 1966). However, both *T. venezuelensis* and *C. accedens* possess additional features that do not occur, or occur only rarely, in *Tridax* and *Galinsoga*. These are the white to creamy yellow corolla color; paniculate capitulescence; angular disc achenes; and the cylindrical to subcampanulate involucre that characterize *Cymophora*. *Tridax venezuelensis* differs from *Tridax* proper in achenes glabrous to strigose, not densely long villous or pilose; pappus of fimbriate scales rather than plumose bristles; and heads less than 8 mm diameter. The transfer of *T. venezuelensis* to *Cymophora* is made on the basis of these morphological comparisons.

Cymophora venezuelensis (Arist. & Cuatr.) Canne, comb. nov.

Tridax venezuelensis Aristeguieta & Cuatrecasas, Flora de Venezuela 10:694. 1964. TYPE: VENEZUELA: Miranda, La Providencia, Sep 1936, *H. Pittier 13754* (HOLOTYPE, VEN; ISOTYPES, F! US!; PARATYPES, *V. M. Badillo 271, 772,* VEN; *H. Eggers 13508,* US!; *H. Pittier 11152,* GH! NY! P! US!).

Additional specimens examined: VENEZUELA: Distrito Federal, between Naiguatá and Hacienda Cocuizal, 7 Oct 1966, *J. Steyermark 97465* (F); above Chichiriviche, 1 Jul 1966, *J. Steyermark* & *L. Aristeguieta 122* (NY, US). State and locality unknown, 9 Aug 1891, *H. Eggers 13568* (US); 1865, *Moritz s.n.* (BM).

Cymophora venezuelensis is distinguished from the other three species in the genus by its pistillate ray florets with corollas having short inner lobelets. The peripheral florets of other species are perfect and have inconspicuously ligulate corollas. *Cymophora venezuelensis* differs in distribution as well, being known only from northern Venezuela, whereas other species of *Cymophora* occur in south central Mexico.